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Plant functional indicators of vegetation response to climate change, past present and future: I. Trends, emerging hypotheses and plant functional modality☆

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ABSTRACT

Plant functional traits are widely applied in models that simulate the effects of climate change on biodiversity and resource management. Here the aim is to examine the potential role of specific plant functional traits and their whole-plant syndromes (Plant Functional Types or PFTs as specific 'modal' trait assemblages) as indicators of vegetation response to climate change, past, present and future. Because plant functional characteristics have evolved through time, it is widely argued that models of vegetation performance under future climates should benefit from a study of plant response under previous climates. This paper presents an overview first, of developmental concepts underlying the current use of PFTs as indicators of plant response to environmental change, second, implications arising from species acclimation and third, process-based models used in reconstruction of vegetation under mainly Holocene environments but also with respect to present and future climates. In this regard the role of individual functional traits in 'biomization' procedures in vegetation response models is briefly discussed. It is concluded that, while PFTs possess limited indicator value at biome scale, uncertainties in the delimitation of local paleohabitats greatly restrict their use as indicators for paleovegetation reconstruction at community level. Emerging hypotheses are: 1) A whole-plant system of modal PFTs based on a novel set of functional traits can provide an improved alternative to PFTs and traits used in models of vegetation response to climate change, 2) Modal PFTs are potentially more efficient indicators of vegetation response to climate change than individual traits, 3) Improved plant functional selection criteria can lead to more efficient parameterization of Earth System and Dynamic Global Vegetation Models.

1. Introduction

The world's natural resources and biodiversity continue to diminish in response to climate change, concomitantly with increasing land use and human population pressure. Faced with these prospects, sustainable resource management requires science-based indicators that can support bioregional planning to mitigate the impact of such change on land cover and the living resource. While most current research focuses on contemporary plant–climate relationships, it is widely considered that an understanding of vegetation response to past climates may provide useful insights into present and future vegetation response to climate change (Williams et al., 1998; Greenwood, 2005; Royer et al., 2007; Aizen and Ezcurra, 2008; Jordan, 2011; Roth-Nebelsick and Konrad, 2018, this volume). This paper considers first, the extent to which plant functional traits may be useful indicators of vegetation response to climate change under mainly Holocene environments and second, explores the degree to which these and functional traits in extant vegetation might serve as common indicators of vegetation change in both contemporary and future climates. Plant functional traits that are commonly applied in process-based models are limited by a paucity of reliable data across varying time scales (Butler et al., 2017). Partly for this reason there is a general reliance on empirical, correlative studies of biophysical data of variable quality which lack consensus in selection criteria (Gillison, 2013). Questions therefore arise as to the kinds of data that are best suited to such purposes and their methods of acquisition and analysis. In order to address these questions the aim of this paper is to examine the potential of specific plant functional traits and their whole-plant syndromes (Plant Functional Types or PFTs) as indicators of vegetation response to climate change past, present and future.

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Advances in understanding the ecology of plant–environment relationships evolved mainly in the Western world where seeking an improved understanding of the relationship between plant traits and climate has remained a central theme of ecology since Theophrastus (370–285 B.C.) first observed weather-related changes in plant and animal behaviour (Hort, 1916). Fastforward to the nineteenth century when Andreas Schimper (1903) coupled plant physiology with adaptation to environment and noted in particular the influence of temperature. His remarkably prescient observation that "A knowledge of the extreme temperatures of a function is more important, in geographical botany, than is that of the absolute optimum.." is a well established theme in modern process-based models of vegetation dynamics and climate change. In the twentieth century, links between plant adaptation and climate became evident in classifications of plant life forms, mostly with respect to seasonality (Du Rietz, 1931; Warming, 1909; Raunkiær, 1934; Iversen, 1936).

Many subsequent studies couple life forms with climate (Buell and Wilbur, 1948; Dansereau, 1951; Fosberg, 1967; Mueller-Dombois and Ellenberg, 1974; Orshan, 1983; Danin and Orshan, 1990; de Bello et al., 2005 Saatkamp et al., 2010). Terminological confusion nonetheless reigns between adaptive 'life form' (*sensu* Raunkiær, 1934) and the more structural-physiognomic 'growth form' (*sensu* Küchler, 1973; Barkman, 1988). Ambivalent use of both terms (Brooks et al., 1997; Körner, 1994; Broennimann et al., 2006; Körner and Jeltsch, 2008; Kleinebecker et al., 2010; Tang et al., 2012; Schellenberger Costa et al., 2018) suggests that any resolution of this basal terminology is unlikely in the short term. Because Raunkiærean 'life forms' are based primarily on the position of the perennating bud during the most unfavourable season (typically a European winter), they carry more functional information than indeterminate 'growth forms' such as 'tree' and 'shrub' that defy adequate and consistently repeatable discrimination especially within a functional context. Yet uncritical use of such terms is widespread in paleoecological and contemporary literature about vegetation response to climate.

Most global vegetation classification and mapping systems (e.g. Schmithüsen et al., 1968; Gaussen, 1945; Walter, 1973; Olson et al., 2001; Schultz, 2002) invoke climate as a proximal driver of plant adaptation and then often as a proxy for mapping 'potential' vegetation types. While such typologies are of value at regional scale, they lack the detail needed to support ecological investigations at local ecosystem or plant community level – a significant factor when assessing plant-based indicators of vegetation response to climates both past and present. For such purposes Fosberg (1967) proposed the inclusion of a vegetation classification system based solely on plant functional criteria as a means of avoiding circularity inherent in terms such as location and environment.

2. Plant functional types and traits

How vegetation adapts to environmental change is one of the primary questions in vegetation science. A wide-ranging focus on differing elements of plant function is evident in studies ranging from the biomolecular to global plant–climate response models. Today, most studies seek to improve theoretical and practical understanding of plant function with respect to ecosystem processes (Table 1) rather than re-designing traditional vegetation classification systems that rarely apply to ecosystem management. Modern day plant functional ecology has its roots in much earlier work (notably Schimper, 1903; Warming, 1909; Du Rietz, 1931; Raunkiær, 1934). Although early twentieth century ecologists were aware of the ecological significance of plant functional characteristics in vegetation dynamics, progress in establishing cause and effect was constrained by a lack of supporting ecophysiological information and technology. In the twenty-first century attention has changed from a focus on vegetation physiognomic-structural features to attributes that reflect plant functional strategies of resource acquisition and conservation (Westoby et al., 2002; Wright et al., 2007; Gillison, 2013, 2016). Within these strategies, different sets of individual plant functional traits, especially those described as orthogonal or independent, are now well established in a global leaf economic spectrum (LES), (Wright et al., 2004) and a leaf–height–seed (LHS) strategy (Westoby, 1998). While the core traits in LES exhibit a generally linear response to key climate factors (e.g. temperature and precipitation) at biome scale (Wright et al., 2004, 2007), they are generally lacking in sensitivity at the community level (see Garnier, (this volume) for an example with respect to water availability). It is at this level, however, where an understanding of plant adaptation to environment is fundamental to predictive and retrodictive modeling of vegetation response to climate change.

Due to their simplicity, and as applied at the macro-scale, the orthogonal or independent traits identified in LES and LHS type strategies have the added attraction that they should, in principle, apply to paleoclimates and, potentially, paleovegetation reconstruction. However, their positioning along a latitudinal and related climate gradient, although inferred at biome level (Wright et al., 2004), has not been shown directly at ecosystem or community scale (Gillison, 2018). As applied in 'biomization' (5.2 below), biomes are characterized by PFTs typically described as grasses, shrubs, broad-leaved or needle-leaved trees, or further 'refined' according to climatic region 'tropical temperate boreal' and graminoid photosynthetic (C_3, C_4) pathways (Woodward et al., 2004; Butler et al., 2017; Huntingford et al., 2017). The more recent trend towards the use of functional traits in predictive vegetation models at global scale is supported by Mucina (2018a) who argues for "..an application of functional syndromes rather than species-based approaches as an effective tool for solving problems of biome ecology, both in predictive and retrodictive modeling of mechanistic as well as functional biomes". The question remains however, as to how such trait syndromes should be constructed according to ecophysiological rather than structural-physiognomic (growth form) criteria and deployed across multiple scales from plot to biomes.

Rapid advances in plant ecophysiology have led to greatly improved biophysical (biotic and abiotic) databases that facilitate the conceptual development and application of plant functional traits and their assemblages as plant functional types (PFTs) (Gillison, 2013) (see Gillison, this volume). A pervasive lack of consensus is evident in the definition of PFTs and functional traits that range from PFTs as 'functionally similar plant types' (Box, 1996), to 'sets of species showing similar responses to the environment and similar effects on ecosystem functioning' (see also Smith et al., 1992; Pillar, 1999; Díaz and Cabido, 1997, 2001; Lavorel and Garnier, 2002; Pillar and Sosinski, 2003) and traits as 'any measurable features at the individual level affecting its fitness directly or indirectly' (Albert et al., 2010). Following Albert et al. (2010) with reference to fitness, as defined by Gillison (2013) and applied here, PFTs are 'any measureable plant trait combinations with potential to influence whole-plant fitness'. This definition is applied to specific assemblages of individual functional traits or analogous plant functional elements (PFEs), (Gillison, 2002, 2013).

Estimates of whole-plant fitness are generally considered to be the product of performance traits such as growth, reproduction and survival (Geber and Griffen, 2003; Violle et al., 2007). Distinctions between functional and performance traits and between performance and fitness components can be difficult and subjective (Geber and Griffen, 2003). Few studies have been able to adequately evaluate the determinants of fitness from a time-integrated and whole-plant perspective involving multiple traits (Reich et al., 2003; Lüttge, 2008; Herrera, 2009; Muscarella and Uriarte, 2016; Shipley et al., 2016). As applied in this paper and as indicated by Schulze (1982) 'fitness' must be considered at whole plant level e.g. where carbon allocation strategies are accounted for in terms of photosynthesis, biomechanical support, transport, nutrient and water acquisition as well as regeneration and reproduction. In this context, individual trait influence on fitness will be a function of the degree to which it is adapted to a particular environmental niche or habitat 'filter' (Craven et al., 2018; He and Biswas,

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Table 1
PFT and trait indicators of terrestrial ecosystem processes and properties[#].

Ecosystem processes and properties	Laboratory, airborne and remote sensing, (mainly quantitative)[*]	Field measurements (qualitative, quantitative)
Productivity (NEP, aNPP, SANPP)	SLA, LAI, Leaf dry matter content (LDMC), LNC, NDVI, SLAR, MODIS, FLORA, hyperspectral imaging	Life form, growth form, canopy height, cover %, basal area all woody plants, root type and depth, bryophyte, lichen cover-abundance of morphotypes, species and PFT diversity, mycorrhizal diversity
Gross Primary Production (GPP) (above ground)	NDVI, MODIS spectra, SIF, SLAR, PRI, Light Use Efficiency (ε), eddy flux	Life form, growth form, canopy height, cover %, basal area all woody plants
Carbon assimilation and investment	Leaf N, P, photosynthetic light response curves, stem and leaf saturating pulse fluorescence, SLA, Specific leaf weight (SLW), leaf area index (LAI), optical functional type, photosynthetic pathway (C_3, C_4, CAM), RCC, NDVI, MODIS spectra, SIF, SLAR, PRI, Light Use Efficiency (ε), eddy flux	Life form, growth form, relative growth rate (RGR), leaf phenology, leaf type (e.g. needle vs. broadleaf, hardness, color), green main stem, water storage, root diameter, bryophyte, lichen cover-abundance of photosynthetic types (C_3, C_4, CAM where known)
Respiration, decomposition	LDMC, leaf N, P, base content, phenolics, SLA, mycorrhizae, stomatal & stem lenticel conductance, C:N, lignin content, lignin:C	Leaf (size, inclination), phenology, litter depth and type, RGR, RNC, SRL, leaf turnover rate, bryophyte, lichen cover-abundance of types
Water use, hydrology	Stomatal conductance, xylem water potential, WUE, SLA, LDMC, wood density, hydraulic conductivity	Life-form, growth form, plant height, basal area, diameter increment, leaf (size, inclination, palisade distribution, phenology, succulence), green stem, root (type, depth, architecture), bryophytes, lichens
Drought resilience (tolerance, avoidance)	SLA, xylem water potential, WUE, stomatal distribution, NDVI, FLORA, MODIS spectra	Canopy height, leaf (size, inclination, phenology, palisade distribution, succulence), root depth, stem:root ratio, green stem, furcation index, growth form, life-form, clonality, leaf longevity, poikilohydry
Tolerance to flooding, tidal movements etc.	Succulence index	Life form, adventitious rooting, salt glands, propagule dispersal, lenticels, succulence, aerenchymatous tissue
Evapotranspiration	Stomatal conductance, xylem water potential, canopy temperature	Growth rate, root depth, root architecture, leaf (size, inclination, thickness, palisade distribution, phenology, succulence, pubescent lamina)
Nutrient stocks, N mineralization, soil fertility	Leaf dry matter content; leaf N, P, mycorrhizal fungi, SLA	Trait size, growth rate, litter depth, bryophyte, lichen composition, Mean canopy height, basal area, lichen cover-abundance, functional modi
Stress-tolerance, ruderal pioneers (C–S–R)	Leaf carbon content, Leaf dry matter content, SLA, Succulence index, leaf inclination	Clonality, canopy height, necromass persistence
Disturbance: Loss of plant biomass and / or species and PFTs (functional modi)	Standing biomass, NDVI, FLORA, MODIS Bands, SLAR	Stem and canopy structure, basal area, furcation index, life form, growth form, seed dormancy, seed dispersal, resprouting ability, vegetative spread, species and PFT counts, species: functional modi to richness ratio, bryophytes, lichens
Response to grazing, herbivore, folivore resistance and defence	SLA, palatability, standing biomass, Leaf N, P, phenolics, RTD	Canopy height, cover %, Vegetation structure, life form, including rosette form, growth form, species turnover, mechanical defence (e.g. thorns), chemical (toxins)
Response to fire	Flammability, ignition testing, NDVI, MODIS, FLORA spectra	Life form, above and below ground storage organs, resprouting capacity, seed bank availability and persistence, seedling establishment, bark types, leaf volatiles, fuel load, clonal regeneration
Response to salinization	SLA, LWC, succulence index, MODIS spectra, NDVI	Life form, growth form, tree height, leaf (succulence, inclination, thickness, palisade distribution) furcation index, green stem, known photosynthetic pathways (e.g. CAM), biocrusts (bryophytes, lichens)
Competition for light	SLA, RGR (seedling)	Plant height, leaf size, type, inclination, crown diameter, tiller increment, vegetative regeneration, seed size, type
Biodiversity	Functional diversity, functional complexity, mycorrhizal fungi	Functional types (e.g. modi), species richness, species composition, bryophyte, lichen cover-abundance of morphotypes
Population demographics, successional dynamics	Photosynthetic rate, RGR, leaf (N, P) mycorrhizal fungi, functional diversity, functional complexity	Life form, growth form, canopy height, basal area, species composition, species richness, functional modi; seed bank and establishment from seed
Invasive potential of vascular species	Leaf construction cost, leaf N & C:N ratio, RGR, SLA, leaf phenolics, A_{max}, PNUE, trait coordination	Life form, growth form, canopy height, basal area, species composition, species richness, functional modi

[#] Modified from Gillison (2013).

[*] Includes instrumentation used to measure gas fluxes, xylem water potential, light dynamics etc. in field. Abbreviations: Amax = net photosynthetic capacity, aNPP = net annual primary productivity, C = Carbon, FLORA = hyperspectral imaging, LAI = leaf area index, LDMC = leaf dry matter content, LNC = leaf nitrogen content, LWC = leaf water content, MODIS = Moderate Resolution Imaging Spectroradiometer. N = Nitrogen, NDVI = Normalized Difference Vegetation Index, NEP = net ecosystem productivity, NPP = net primary productivity, P = Phosphorus, PNUE = photosynthetic energy use efficiency, PRI = Photochemical Reflectance Index, RCC = Root construction cost, RGR = relative growth rate, RNC = Root N concentration, RTD = Root tissue density, SANPP = specific annual net primary productivity, SIF = Sun Induced Fluorescence, SLA = specific leaf area, SLAR = Side Looking Airborne Radar, SLW = specific leaf weight, SRL = Specific root length, WUE = water use efficiency. See Gillison (2013, Table S12.2); Gillison et al. (2016) for units used by different authors.

2018; Li et al., 2018a; Medeiros et al., 2018) as well as the extent to which its function is mediated by other traits internal and external. The assumption that specific trait assemblages can represent a measure of plant 'fitness' and a capacity to adapt to environmental change is a common thread in a number of developments towards a functional typology (Keddy, 1992; Boutin and Keddy, 1993; Gillison and Carpenter, 1997; Lavorel et al., 1997, 1999, 2007; Díaz et al., 2002; Gillison, 2013).

An initial, holistic 'whole-plant' typology, as distinct from one defined by singular trait descriptors (Gillison, 1981) was based on syndromes or functional '*modi*' composed of assemblages of 'Plant Functional Attribute (PFA)' leaf traits and mainly life forms shown to

respond to soil properties. This development was paralleled by the structural-functional types of Box (1981, 1996), who defined phenophysiognomic plant types associated with ecophysiological functional traits that could be related directly to climate variables such as water balance and evapotranspiration (see also Box and Fujiwara, 2005; Box, this volume).

3. Acclimation of plants to changing climate

Acclimation is the process in which an individual organism adjusts to a change in its environment (such as a change in elevation, temperature, humidity, photoperiod, or soil properties), allowing it to maintain performance (functional fitness) across a range of environmental conditions. Because acclimation adds a significant element of functional complexity to plant fitness under climate change, a consideration of acclimation pathways is relevant to the choice of plant functional indicators of plant and vegetation response. Evidence of acclimation is widely manifested across differing levels of plasticity where phenotypic changes including ontogenetic adjustment to environmental change can be diagnosed according to specific plant functional traits (Abakumova et al., 2016; Gillison, 2013, 2016; Baird et al., 2017). At global scale, under a warming climate, plant community response to acclimation pressure will be widespread but is likely to be most evident among plant individuals in marginal habitats represented in high elevation, high latitudes and high temperature (arid) extremes. Within and between species and habitats, functional traits may vary in relation to the extent that the plant succeeds in acclimating to ambient conditions. Here, overall sensitivity (or resistance) to environmental change is determined by the plant's physiological plasticity as indicated by its ability to alter its structure and functions in order to react to total oxidative pressure (Bussotti, 2008). Such sensitivity can vary significantly for example among certain Cactaceae where response to heat stress is offset by the capacity of individuals to generate antioxidants that, in turn will be a function of the level of protection offered by anatomical or morphological traits (Nuzhynaa et al., 2018). An underlying challenge therefore is to identify which traits, when combined in a whole plant, offer the best means of forecasting acclimation response to climate change at individual plant and community scale. A general lack of uniformity in such methodology is evident in a study of two American fog deserts by Larraín-Barriosa et al. (2018) who found that despite a strong community convergence in vegetation structure, certain traits inevitably differed among deserts, suggesting the need to expand the fine scale study of plant trait convergence in such environments. In a wide-ranging overview of acclimation processes in relation to oxidative stress in trees, Bussotti (2008) found that the capacity of plants for temperature acclimation of photosynthesis varied with metabolic pathway: (1) C_3, C_4, and CAM species; and (2) functional types within C_3 plants that generally had a greater ability for temperature acclimation of photosynthesis than C_4 and CAM plants across a broad temperature range. CAM plants on the other hand, acclimate day and night photosynthetic process differentially to temperature, and C_4 plants are better adapted to warm environments than C_3. Moreover, within C_3 species, evergreen woody plants and perennial herbaceous plants can show greater temperature homeostasis of photosynthesis than deciduous woody plants and annual herbaceous plants (Yamori et al., 2014).

Carboxylation pathways may also vary in the way they perform in shade versus sun environments. Acclimation to shade by the climbing CAM plant *Hoya australis* for example, is indicated by thinner leaves, increased chlorophyll content, decreased chlorophyll *a/b* ratios, lower dark respiration rates, and lower light compensation points (Adams et al., 1988). Although light-dependent increase in foliage photosynthetic capacity per area can be similar in different PFTs, they can also be shown to differ fundamentally in the way constituent traits interact to mediate photosynthetic capacity where different trait combinations within PFTs are responsible for within-canopy photosynthetic acclimation (Niinemets et al., 2015). Acclimation in carboxylation pathways is not restricted to leaves. Stem based (cortical) photosynthesis is widespread among vascular plant species including many 'leafless' succulent species, and acts as a significant complement to foliar photosynthesis through refixing internal metabolic carbon (Gibson, 1996; Pfanz, 1999; Lüttge, 2008; Ávila-Lovera et al., 2017). In studies of the bark of the olive tree (*Olea europaea* L.), Filippou et al. (2007) recorded low chlorophyll *a/b* ratio and light compensation points in olive stems with low phellem light transmission, in accordance with a shade acclimation hypothesis, concluding that olive tree bark possesses an efficient photosynthetic mechanism that may significantly contribute not only to the reduction in concentrations of CO_2 in the inner bark, but also to whole-tree carbon balance. Similar support for the sun–shade acclimation hypothesis is recorded in a study of the shrub *Morella cerifera* in the Barrier islands of the SE USA (Vick and Young, 2009) and in Canadian *Acer saccharum* and *Betula alleghaniensis* where, in the latter, light-driven acclimation of leaf photosynthetic capacities was closely related to variation in leaf nitrogen and leaf mass per area and where fine-scale physiological adjustments were observed during seasonally driven acclimation of leaves (Delagrange, 2011) (see Sect. 8 below).

At the whole plant level, capacity for acclimation inevitably depends on the interaction of multiple traits. Leaf longevity for example, is known to be coupled with decreasing plasticity in a Panamanian forest (Valladares et al., 2000) while among tree species in Bolivian seasonally dry forests, there is evidence for lower light-related plasticity than in wet forest species, probably because wet forests cast deeper shade (Markesteijn et al., 2007). In Borneo, leaf area-based photosynthetic traits were associated with tree height and the degree of leaf drought stress, even in diverse tropical rain forest trees (Kenzo et al., 2015). There is additional evidence that acclimation within communities may be influenced by vegetation structure and the composition of growth forms. A study in a Gabonese rain forest (Kazda and Salza, 2000) found that, when nitrogen was expressed on a leaf area basis, differences in nitrogen concentration between liana and tree leaves were reversed for the most shaded sites. In the tropical dry forests in India, Vivek and Parthasarathy (2018) found that trait values for SLA and mass based leaf N were much higher in lianas than trees suggesting a competitive advantage in acclimation to disturbance. Gas exchange via leaf stomatal pathways has a direct influence on photosynthesis. As shown by Bucher et al. (2017), herbaceous species in temperate climates with few but large stomata tended to adjust stomatal size across environmental gradients, whereas species with small but many stomata mainly adjusted stomatal density. Importantly, Bucher et al. (2017) also found that amphistomatic leaves showed a preference for high radiation and air mass exchange with higher water use efficiency and concluded that these traits, together with the distribution of stomata between the two sides of the leaf, indicate how species optimize carbon uptake and balance water loss and radiation gain. Apart from their obvious significance for acclimation, these findings and similar studies, provide valid scientific support for the use of dorsiventral and amphistomatic or isobilateral leaf types in the present application of modal PFTs (Section 8 below).

Recent evidence indicates that metabolic acclimation is possible, but far from universal among species – findings that do not support a common practice in Dynamic Global Vegetation Models (DGVMs) of assigning fixed leaf trait values to PFTs where, according to Bloomfield et al. (2018), trait-based models should allow for interspecific differences, together with spatial and temporal plasticity in leaf structural, chemical and metabolic traits. High-temperature tolerance in plants is important in a warming world, with extreme heat-waves predicted to increase in frequency and duration, potentially leading to lethal heating of leaves. Global patterns in high-temperature tolerance of leaf metabolism were analysed by O'Sullivan et al. (2017) using predicted heatwave events for 2050, where, accounting for possible thermal acclimation, their models predicted that safety margins could shrink in a

Table 2
Distance matrix of inter-modal PFTs showing intraspecific variation within Stone Birch *Betula ermanii*[*].

Modal PFT	mi-pe-do-de-ph	no-co-do-de-ph	no-la-do-de-ch	no-la-do-de-ct-ph	no-pe-do-de-ct-ph
mi-pe-do-de-ph	–	–	–	–	–
no-co-do-de-ph	3	–	–	–	–
no-la-do-de-ch	6	5	–	–	–
no-la-do-de-ct-ph	6	5	6	–	–
no-pe-do-de-ct-ph	4	5	8	2	–
no-pe-do-de-ph	1	2	5	5	3

* Lower half of a distance matrix generated by VegClass based on transformational values between modal elements derived from Gillison and Carpenter (1997). Refer SI Table 2, Fig. 3 for PFT detail.

warmer world, as rising temperatures are likely to exceed thermal tolerance limits. Thus, increasing numbers of species in many biomes may be at risk as heat-wave events become more severe with climate change. Upper canopy dark respiration and temperature dependencies were examined by Huntingford et al. (2017) who modeled aggregates of dark to whole-plant respiration. Their analyses found similar trends in warming effects on acclimation to those indicated by O'Sullivan et al. (2017) with increases in whole-plant respiration for preindustrial estimates and decreases for mid-latitudes while acclimation lowers this for the tropics, with increases elsewhere such that global whole-plant respiration could be around 30 percent higher than current estimates under existing GCMs. Acclimation in contemporary and future climates may be determined more by adaptation to paleoclimates than previously thought. Slow community assemblage dynamics of paleovegetation were consistent with paleoclimate predictors that were found by Blonder et al. (2018) to greatly improve prediction of contemporary plant functional composition compared to contemporary climate predictors. Further, when compared to certain gymnosperms that evolved adaptive characteristics under highly variable environments, global success of angiosperms appears tied to a small set of alternative solutions when faced with a novel environmental threshold (Zanne et al., 2018).

4. PFTs, climate change and paleovegetation reconstruction models

As with many contemporary models of vegetation response to climate, there is an evident need for improvements in paleoclimate models, species paleodistribution data and model validation together with rigorous modeling methods including mechanistic models of paleoenvironmental reconstruction (*cf.* Franklin et al., 2015). The past decade has seen a rapid development of dynamic process-based models of land surface response to climate change. Among these are atmospheric general circulation models (AGCMs) used in weather and climate prediction or Earth System Models (ESMs). These models require correct representation of the biophysical properties of the land surface that together control the fluxes of radiation, sensible and latent heat, and trace gases. Since vegetation mediates all these land surface–atmosphere interactions, its accurate representation is mandatory in such models (Lapola et al., 2008). Earlier equilibrium terrestrial biosphere and DGVMs (Haxeltine and Prentice, 1996; Kaplan, 2001) included relatively crude PFTs such as 'Temperate broadleaf deciduous shrub'. Apart from the very limited functional information carried by such PFTs, their ubiquitous connection with location or climate type is clearly vulnerable to circular reasoning (*cf.* Fosberg, 1967; Woodward et al., 2004). Increasing dissatisfaction with much of the limited and potentially misleading information contained in these 'biomic' types of PFTs (Sakschewski et al., 2015; Verheijen et al., 2015; Yang et al., 2015; Langan et al., 2017) has led to significant improvements in PFT information content for process-based models (Wright et al., 2004; Gillison, 2013; Díaz et al., 2016). Many models are now supported by continuous and process-based trait–environment relations that are consistent with a functional trait-based approach. This, in turn, allows improved calculation of fluxes based on functional characteristics (Van Bodegom et al., 2011; Sakschewski et al., 2015; Yang et al., 2015; Langan et al., 2017).

Dynamic vegetation modeling has contributed significantly to a broader understanding of trait–climate relationships. A major obstacle to the practice of assigning a single trait value to all members of a PFT within a DGVM is that possible sources of variation, such as climate seasonality, are ignored. Moreover, trait-based models need to allow for inter- and intra-specific differences including spatial and temporal plasticity in leaf structural, chemical and metabolic traits rather than fixed trait values (Bloomfield et al., 2018). Recent evidence of intraspecific variation (phenotypic plasticity) along environmental gradients has enhanced awareness that plant functional response to climate change has a potentially more important role in process-based models than previously thought (Read et al., 2017; Wellstein et al., 2017; Bloomfield et al., 2018; Jackrel and Morton, 2018; Li et al., 2018b; Mitchell et al., 2018; Garnier et al., 2018; Ivanova et al., 2018; Lang et al., 2018). A study of European grasslands by Tautenhahn et al. (2019) (this volume) found comparatively small effects of within population intraspecific trait variability that decreased rapidly with increasing number of considered traits compared to such variability between populations, suggesting that intraspecific trait variability is mainly driven by environmental effects rather than local biotic interactions and microsite effects – findings that may have future implications for population modeling within DGVMs. An example of intraspecific variation within a widely distributed species such as *Betula ermanii* is an indication of how such variation can be detected in a modal PFT (Table 2, Fig. 1) (See also Gillison, this volume). From these studies it is abundantly clear that long-term forecasting of vegetation response to climate change needs to accommodate short-term inter- and intra-specific functional response patterns to periodic phenomena such as seasonality as well as differential rates of species acclimation. Here, phenotypic adjustment is an important driver of short-term functional plant response to climatic extremes such as drought, where differential reactions of functional groups have to be interpreted against the background of the group's evolutionary configuration that, in turn, can differ between climatic zones (Wellstein et al., 2017). Where paleo documentation is confined to relatively few taxa, more recent developments in spatial distribution modeling (SDM), sometimes referred to

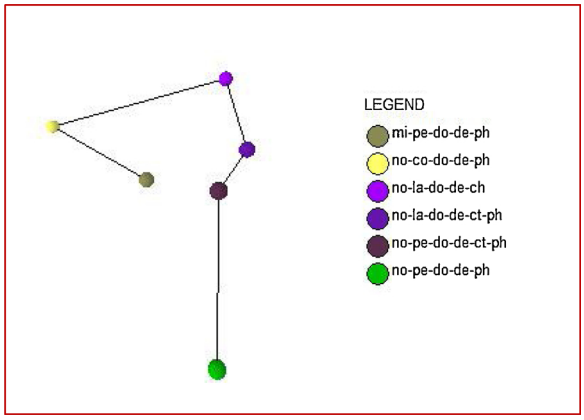

Fig. 1. An example of intraspecific variation within Stone Birch *Betula ermanii* illustrated via a minimum spanning tree derived from inter-modal distances (Table 2) and computed using a Bray-Curtis association measure and multi-dimensional scaling. Field data from Kamchatka peninsula, Russian Far East (Gillison, 2012). Variation in modal PFT composition corresponds with variation in site biophysical features. Refer SI Table 2, Fig. 3 for PFT detail.

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as ecological niche modeling, have shown promise. SDM is widely applied in modeling quantitative, empirical, predictive models of species environment relationships and often used to hindcast paleodistributions of species and ecological communities (paleo-SDM, or PDM) (Svenning et al., 2008; Elith and Franklin, 2013; Potts et al., 2013; Franklin et al., 2015; Janská et al., 2017) (see also Carpenter et al., 1993; Gillison, 2013).

5. Biomes and climate indicators

5.1. Biome concepts

Biomes are the primary biophysical and spatial reference unit for vegetation–climate associations worldwide especially with respect to 'hindcasting' or 'retrodicting' past climates. The convergent patterns between vegetation types and climate observed earlier by both von Humboldt (1806, 1811) and Schimper et al. (1903) and the 'life form' ecologists of the early twentieth century, prefaced the biome concept that is now embedded in vegetation ecology. Originally defined by Clements (1916) as a synonym for 'biotic community', biomes have come to represent a biogeographical basal unit, used to organize, describe and compare variation in vegetation complexity at broad regional scales (Mucina and Rutherford, 2006; Rutherford et al., 2006; Mucina, 2018a, b). Despite their ecological limitations at finer geospatial scales, biomes are widely used in global conservation planning, meta-analyses, and Earth System Modeling. On the other hand, they are generally regarded as globally convergent vegetation formations similar in structure and function, that explicitly ignore floristic differences and plant species composition (Moncrieff et al., 2016).

As a simply constructed biophysical unit, a biome can provide a broad level of generality for geographical purposes that facilitates cross-regional comparisons where environments may be similar but where taxa may differ. While satisfying a general need at this level, biome classifications lack the sensitivity needed for more detailed studies at ecosystem and plant community level that are required in studies of plant response to climate change. Further, the inherent 'fuzziness' of the biome concept (Donoghue and Edwards, 2014) and its real-world application, continue to challenge consensus in biome definitions worldwide (Lehmann et al., 2014; Higgins et al., 2016; Moncrieff et al., 2016). One of the most common biome classifications, namely that of Walter (1973), includes zonobiomes classified primarily according to climate, that with few exceptions, may correspond to soil type and / or zonal vegetation. Among early pseudo-biome constructs are 'life zones' based on climatic zones characterized by species (Merriam, 1898), and Whittaker's (1975) 'biome-types' based on temperature and precipitation with evident affinities to Holdridge's (1967) Life-zones. These and other biome classifications (Olson and Dinerstein, 2002; Schultz, 2002, for example) are similarly classified according to both climate and vegetation structure. The "ecosystems or biomes" of Goodall (1974) on the other hand, are primarily based on vegetation structure with only minor climatic and phenological tags.

Biomes defined by Woodward et al. (2004) (according to non-Raunkiærean "life forms" and based on remotely sensed leaf longevity and morphology) typically combine plant traits with climate (e.g. 'Broadleaf cold deciduous') but also include functionally distinct graminoid photosynthetic pathways (C_3, C_4) at finer scale. The potential for biomes to be described as a 'functional biome' according to more specific functional criteria has been proposed by Mucina (2018b). Despite continuing debate on their methods of construction, the scale at which biomes are applied renders them attractive as referable units across certain broad spatio-temporal scales. Woodward et al. (2004) for example, argue that the "global spread of grasses, a new 'superbiome', was probably initiated 30–45 Myr ago by an increase in global aridity, and was driven by the natural spread of the disturbances of fire and animal grazing". Nonetheless, according to Woodward et al. (2004), both location and climate as used to define biomes should be avoided when investigating the geographical distribution of biomes as this leads to circularity in which climate itself defines the distribution of a biome and thus contributes to a self-fulfilling prophecy. Despite their lack of precision at ecosystem level, biomes remain one of the key vegetation units in paleoecology.

5.2. 'Biomization'

Biomization is a procedure in paleoecology that is commonly used to simulate models of plant response to climate change. The method typically assigns pollen taxa to one or more plant functional types (PFTs) described by Prentice et al. (1996) as "..broad classes of plant defined by stature (e.g. tree / shrub), leaf form (e.g. broad-leaved / needle-leaved), phenology (e.g. evergreen / deciduous), and climatic adaptations". Biome models typically construct PFTs according to specific plant structural-physiognomic and environmental attributes and 'let' the physical environment select (a) those PFTs that can survive, grow and reproduce, and (b) among these PFTs, those that can dominate (e.g. trees over shrubs). Biomes are then defined according to which PFT(s) are "dominant". Prentice et al. (1996) assert that the PFT concept "can also provide the basis for an objective method to derive global paleobiome distributions from palaeoecological data, such as pollen and plant macrofossil records." The Prentice-type PFTs are then assigned to their respective biomes and affinity scores calculated for each biome (sum of the square roots of pollen percentages contributed by the PFTs in each biome). First developed for Europe (Prentice et al., 1996), different versions of this method have been applied globally (Jolly et al., 1998; Takahara et al., 1999; Elenga et al., 2000; Tarasov et al., 2000; Thompson and Anderson, 2000; Williams et al., 2000; Pickett et al., 2004; Marchant et al., 2009; Hoogakker et al., 2016; Binney et al., 2017). As originally described by Prentice et al. (1996), the method provides an objective means of relating vegetation pattern to climate at manageable geospatial scales (see also similarly consistent arguments by Tarasov et al., 1998; Elenga et al., 2000; Kaplan, 2001; Marchant et al., 2009; Hoogakker et al., 2016). Typical examples of 'objective' PFTs are 'Warm-temperate sclerophyll shrub' (Prentice et al., 1996) and 'Tropical broad-leaved evergreen tree' (Marchant et al., 2009) with similar classifications by other authors.

To some degree, the PFTs in biomization classifications are analogous to the pheno-physiological plant types of Box (1981, 1996) such as 'Mediterranean dwarf-shrubs'. In each of these cases however, the presumption of objectivity is governed by the subjective selection of biomes and then according to very loosely defined criteria (*cf.* Hoffmann et al., 2012). From a plant functional aspect there is little to suggest from these studies that a biome classification in itself confers a particular functional trait or a trait syndrome to a plant individual. As outlined above, inclusions of extrinsic attributes used in biome-type PFT descriptors (e.g. geospatial and climatic) can contribute directly to circular reasoning (*cf.* Woodward et al., 2004; Moncrieff et al., 2016). Uncertainties with respect to PFT definitions remain embedded in the use of biomization. Possibly reflecting these uncertainties, and despite its wide-ranging application, Elenga et al. (2000) maintain there is as yet no unique and global biomization scheme – a situation that remains unchanged in the present day

6. Functional types and traits as paleovegetation indicators

6.1. Biomized PFTs in paleoclimate and vegetation reconstruction

As indicators of vegetation response under paleoclimates, plant functional traits and PFTs fall into two main streams; one in which PFTs are 'biomized' in process-based models (typically General Circulation Models or GCMs) and the other in which specific plant functional traits are used in multivariate analyses most commonly with extant species-specific pollen types as proxies for paleovegetation reconstruction. In the first stream, environmentally constrained (biomic) PFTs are

included as parameters in dynamic vegetation models such as LPJ_GUESS (Smith et al., 2001; Allen et al., 2010), and in other GCM type model simulations. Among the latter is the unified model (UM) of the HadCM3 – a GCM originally consisting of coupled atmospheric model, ocean, and sea ice models (Gordon et al., 2000; Pope et al., 2000; IPCC, 2007; Allen et al., 2010) that has since undergone significant modifications (Allen et al., 2010; Valdes et al., 2017). FAMOUS (Smith, 2012), an Earth System biogeochemistry–biogeography model, derived from HadCM3 and BIOME4, (Kaplan et al., 2003), predicts global vegetation distribution (further details in Hoogakker et al., 2016; Valdes et al., 2017). In these models PFTs are allocated values according to their known or assumed response characteristics to key climate, substrate and remotely sensed variables (e.g. temperature, precipitation, insolation, soil texture, depth, and atmospheric CO_2, CH_4, N_2O, leaf area index (LAI), annual net primary production (aNPP), normalized difference vegetation index (NDVI), canopy conductance, photosynthesis, respiration, and phenological state) (Kaplan et al., 2003; Hoogakker et al., 2016; Moncrieff et al., 2016). The allocation of extrinsic attributes in this way, does in itself, raise questions about potential circularity in PFT selection criteria.

In paleovegetation reconstruction, biomized PFTs are most frequently used to generate specific vegetation types (e.g. Tundra). Distinctions between such types are considered potentially important for estimating feedbacks involving changing water and carbon exchanges, as vegetation types can differ greatly in their biogeochemical and biophysical characteristics including the height of perennial biomass and aNPP (Bigelow et al., 2003). Many paleoclimate data and modeling studies focus on the contrasts between the Last Glacial Maximum (LGM 21.5 ka BP), the mid-Holocene (6 ka BP), and the pre-industrial period (Hoogakker et al., 2016), with output typically expressed as mapped vegetation types. These are exemplified in the Palaeovegetation Mapping Project (BIOME 6000; Prentice and Webb, 1998) that produced the first maps of reconstructed vegetation distribution across the northern high latitudes and where subsequent mapping has produced informative broadscale comparisons between paleoclimate and contemporaneous conditions (Bigelow et al., 2003) (SI Fig. 1). Other examples of biome-based vegetation reconstruction maps are the product of the Cooperative Holocene Mapping Project (Webb, 1985; Li et al., 2014). These and additional references to biomized PFT simulations are listed in Table 3.

6.2. Plant functional traits as indicators of paleovegetation

The identification and characterization of plant functional traits under paleoclimates is at best a form of forensic or 'dark' ecology where inferences are often drawn from the most marginal of evidence. Traits are often compared with speleothem, clastic flux and archaeological data to assess the influence of moisture balance, glacial activity and human impact on vegetation (Reeves et al., 2013; Valencia et al., 2018). In most cases, paleotraits are calibrated against taxa and growth forms either known or assumed to possess similar functional traits in extant vegetation. Foremost in the list is fossil pollen, often in company with pteridophyte spores, charcoal (both micro- and macro), phytoliths, *Pediastrum* (Meyen) (algae) and a range of leaf morphological characteristics including especially leaf margins (entire and non-entire) and size (area). Derivative species-based traits extend to taxonomic groups as well as phenological, genetic and diversity measures. (See also SI Table 1 for a more detailed treatment of plant functional traits in the context of paleoclimate and paleovegetation habitat definition). The following functional traits in common use in paleoecology are each briefly reviewed with respect to their potential indicator value for paleovegetation reconstruction:

6.2.1. Trait-related biomarkers

Various types of trait-related biomarkers for paleoclimates employ stable isotope ratios of different elements using radiocarbon dating with carbon and oxygen and nitrogen isotope data (^{14}C, $\delta^{13}C$, $\delta^{18}O$) (Brooks et al., 1997; Reeves et al., 2013; Woodruff, 2003; Williams et al., 2014; Werth et al., 2015; Yang et al., 2015; Hultine et al., 2016). Isotopic oxygen $\delta^{18}O$ is used to establish timelines for foraminifera in marine sediments (Woodruff, 2003), while leaf isotopic nitrogen ($\delta^{15}N$) on the other hand, is widely used in modern ecology (Schulze et al., 1998; Hoffmann and Franco, 2003) although rarely in terrestrial paleoecology. However, isotopic nitrogen is also a biomarker for marine planktonic chlorophyll where isotopic depletion of chlorophyll, a relative to total algal nitrogen (*cf. Pediastrum*), is a robust relationship that justifies the use of chlorophyll as a nitrogen isotopic surrogate for photoautotrophs (Sachs et al., 1999). More detailed information relating to location and time scale of trait usage is contained in SI Table 1.

6.2.2. Fossil pollen

Fossil pollen is by far the most widely used plant trait in paleovegetation reconstruction and pollen-based studies occupy a vast literature. Uncertainties related to taxon identification, pollen and spore dispersal and other limitations involving dispersion, deposition and preservation (taphonomy), impose significant constraints in defining paleohabitats and vegetation assemblages. As a consequence, site-specific plant species composition and diversity (richness) that are well described for many present-day ecosystems, are difficult to reconstruct from the fossil record (Chytrý et al., 2017). Fossil pollen data remain nonetheless key indicators of taxa and paleovegetation reconstruction worldwide and are frequently combined with other fossil plant traits. Where they can be matched with extant pollen and taxa, taxonomic rankings tend to be applied well above genus level or are alternatively keyed to PFTs as in biomization (Kershaw, 1970; Bonnefille et al., 1995; Peyron et al., 1998; Yu et al., 1998; Bonnefille and Chalié, 2000; Nakagawa et al., 2002; Ren and Berg, 2002; Davis et al., 2003; Jiang and Liu, 2007; Li et al., 2008; Marchant et al., 2009; Allen et al., 2010; Jiang et al., 2010; Xu et al., 2010; Li et al., 2014; Blagoveshchenskaya, 2017).

6.2.3. Fossil spores

Unlike pollen from seed plants, fossil spores are produced by algae, mosses, liverworts, ferns and fern allies. They occur in great numbers and are ubiquitous in almost every kind of depositional environment. Their abundance and frequency are a taphonomic function of the proximity and vegetation type of the source area where pollen and spores can be transported up to several hundred kilometers through aerial and fluvial transport (Streel and Bless, 1980; Mishra et al., 2017). Spore deposition is subject to multiple taphonomic constraints such as physical (transportation by air and water, diagenesis), chemical (pH of the sediments, oxidation) and biological processes (predation, biological degradation) (Mishra et al., 2017). Additionally, post-depositional erosion or mass transport of the sediment in which the palynomorphs have been preserved, may rework the sediments into deposits of a stratigraphically different age (Streel and Bless, 1980). Possibly for these reasons, spores involving algae, ferns and aquatic taxa tend to be excluded from analyses of fossil assemblages (Peyron et al., 1998; Li et al., 2014). Depending on the site conditions, certain types of deposits such as peat that enhance preservation, can facilitate identification of certain taxonomic groups such as ferns and fern allies (Blagoveshchenskaya and Isaev, 2018). Most spore classification schemes are keyed to morphological features that are commonly intended to reflect generic taxonomic relationships (Dettmann, 1963; Jäger, 2004). Where identification can be problematic, alternative morphological classifications may be created as described by Jäger (2004) and sporomorphs may be given informal names analogous to operational taxonomic units (OTUs) in numerical taxonomy (Sneath and Sokal, 1962; Esteban et al., 2017; Jardine et al., 2018). Taken together, the factors outlined above mitigate heavily against the accurate description of any original vegetation habitat and thus greatly limit prospects of hindcasting vegetation response to climate change at local

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Table 3
PFTs used in biomization of vegetation reconstruction under varying climates.

PFT*	Region	Time scale	Source
C-L-P-G	Global (potential natural vegetation)	Industrial period	Sitch et al. (2003)
C-L-P-G	Global synthesis. Terrestrial biosphere	> 120 kya	Hoogakker et al. (2016)
C-L-P-G	High latitude biomes ("Arctic ecosystems")	Present day using observed climate, and the LGM, mid-Holocene, and a "greenhouse" scenario for year 2100	Kaplan (2001); Kaplan et al. (2003)
C-L-P-G	High latitude biomes ("Arctic ecosystems")	6000 ^{14}C years BP and 18,000 ^{14}C years BP	Prentice and Webb (1998)
C-L-P-G	Arctic ecosystems north of 55 °N.	Last glacial maximum (LGM) and mid-Holocene (6000 years BP).	Bigelow et al. (2003)
C-L-P-G	Europe and Asia north of 40 °N	21000 → 0 cal yr BP (kyr cal BP; calibrated ages, 1000-year time-slices)	Binney et al. (2017)
C-L-P-G	Northern Eurasia	Early Holocene (42–10 ka BP)	Allen et al. (2010)
C-L-P-G	Northern Eurasia (Former Soviet Union and Mongolia)	Holocene; 6000 BP	Tarasov et al. (1998)
C-L-P-G	Glacial steppic vegetation in Europe	18,000 ^{14}C yr BP	Peyron et al. (1998)
C-L-P-G	Europe: southern part plus Anatolia, Syria and Iran, region north and east of the Mediterranean Sea. Africa: between 10 °N and 32 °S:	18,000 ^{14}C yr BP	Elenga et al. (2000)
C-L-P-G	Africa and the Arabian peninsula.	Mid-Holocene 6000 BP	Jolly et al. (1998)
C-L-P-G-PS	Africa Congo basin	18,000 BP	Izumi and Lézine (2016)
C-L-P-G	Northern China. Deserts between 35–50 °N and 75–125 °E	mid-Holocene (6 ± 0.5 ^{14}C ka)	Li et al. (2014)
C-L-P-G	China 15-55 °N.	Mid-Holocene 6000 BP to present	Yu et al. (1998)
C-L-P-G	Japan and adjacent areas	Contemporary and Late Holocene, 22,000–18,000 BP	Gotanda et al. (2002)
C-L-P-G-T	Japan, Lake Mikata	47000 year sample. Late Quaternary reconstruction	Nakagawa et al. (2002)
C-L-P-G	Western North America	Contemporaneous; 6000 and 18,000 radiocarbon years before present (^{14}C yr BP).	Thompson and Anderson (2000)
C-L-P-G	Eastern North America	Contemporaneous	Williams et al. (1998) (Following Prentice et al., 1992)
C-L-P-G	Sierra Madre Occidental (SMO) in northwestern Mexico	Four Holocene sequences	Ortega-Rosas et al. (2008)
C-L-P-G-S	Latin America from 35 °N to 65° ° W to 120 °W extending from Mexico to islands off southernmost South America from Eastern Brazil to the Galapagos Islands.	Biome changes from the present, 6000 ± 500 and 18 000 ± 1000 ^{14}C yr BP.	Marchant et al. (2009)

* **PFT code**: **C** = climate (e.g. Boreal); **L** = Leaf morphology (e.g. Needle-leaved); **P** = phenology (e.g. evergreen); **G** = Growth or Life form (e.g. Tree, shrub); **PS** = photosynthetic pathway (e.g. C_3,C_4); **S** = structural (e.g. mean canopy height); **T** = Trees only.

community and habitat scales.

6.2.4. *Pediastrum*

Coenobial (fixed cellular colony) green algae belonging to the genus *Pediastrum* (Meyen) are globally distributed in association with freshwater phytoplankton communities, some being cosmopolitan with others restricted to cold, temperate or warm regions. Due to their resistance to decay, many species are found in fossil or subfossil condition as more or less abundant elements of palynomorph assemblages. Records extend from the Early Cretaceous (Evitt, 1963), and their presence in sediments of different ages is generally recognized as one of the most reliable paleoecological markers of freshwater environments, in particular standing water bodies such as ponds and lakes (Tell, 2004; Tell and Zamaloa, 2004; Zamaloa and Tell, 2005; Jiang et al., 2010). According to Komárek and Jankovská (2001, quoted by Zamaloa and Tell, 2005), this worldwide genus is known to comprise at least 24 living species. While some authors match fossil forms to extant taxa (Evitt, 1963), others describe new fossil taxa (Zamaloa and Tell, 2005). Because *Pediastrum* is known only from freshwater, their records in marine sediments are usually a clear indication of previous and quite different environments that have the potential as biomarkers for associated terrestrial vegetation types (*cf*. Evitt, 1963; El Atfy et al., 2017), (SI Table 1).

6.2.5. *Fossil phytoliths*

Many terrestrial vascular plants absorb soluble silica from the soil solution and groundwater that is subsequently deposited within plant cellular structure as microscopic particles of opaline silica ($SiO_2.nH_2O$) known as phytoliths with evidence that Silicon content itself may be considered a plant functional trait (Katz, this volume). When the plant dies and decays, the inorganic phytoliths remain in the sediment as microscopic silica particles of varying sizes and shapes (Thorn, 2006; Nurse et al., 2017). Phytoliths are commonly classified according to their morphology and size following established procedures that include the international phytolith nomenclature system as well as comparisons with published photographs and descriptions (Strömberg, 2002; Madella et al., 2005; Barboni et al., 2010). While a single plant can produce several different phytolith morphotypes, diagnostic plant taxa and distinctive phytoliths are nonetheless being recognised at family, genus, and, increasingly, species level (Mercader et al., 2000, 2009; Pearsall, 2000; Carter, 2002; Thorn, 2006; Nurse et al., 2017). Phytolith analysis is a standard tool in studies of Holocene and Pleistocene paleoecology and archaeology (Piperno, 1988, 1989; Pearsall, 2000; Strömberg, 2002; Strömberg et al., 2007; Guo et al., 2012; Boyd et al., 2013) that can provide insights into past vegetation types and paleoclimates. In North Eastern China for example, herbaceous phytoliths recorded from forest understorey and overstorey as well as grasslands, were used as indicators of paleoclimate reconstruction (Li et al., 2017). Unlike other palynomorphs, phytolith assemblages can also give an indication of the proportion of C_3 and C_4 grasses in the flora thus indicating likely adaptation to ungulates (Strömberg, 2002). In other studies (Sedov et al., 2003) phytoliths in C_3 and C_4 grasses in central Mexico agreed with carbon isotope data indicating plant cover changes driven by wet / dry paleoclimate oscillations. Elsewhere, in the St. Louis River Estuary, Minnesota, USA, combined fossil pollen and phytolith records were used to distinguish between aquatic and upland grasses (Nurse et al., 2017). In Oregon, USA, the ratio of grass and tree phytoliths also helped to confirm the pattern of conifer encroachment on former savanna (Kirchholtes et al., 2015). Overall, phytolith assemblage analysis of soils, buried soils, and sediments appears to be a promising technique in detecting past vegetation changes (Delhon et al., 2003; Thorn, 2006). In South Africa however, phytolith concentration was found to relate mostly to vegetation types and the dominant vegetation rather than soil type (Esteban et al., 2017). (SI Table 1 for further details). Compared to other traits listed here, phytoliths offer some advantages as indicators of paleovegetation. As with other traits that are subject to variation in depositional history however, the application of phytoliths as indicators of taxonomic

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assemblages at a scale below 'vegetation type' level requires further testing.

6.2.6. Macrofossils

Macrofossils are organic plant remains that, while generally visible to the human eye, are usually subject to microscopic analysis. Macrofossil data mostly require supporting palynomorphic evidence in order to reconstruct paleovegetation types. In North America, Thompson and Anderson (2000) found that, while forest biomes were difficult to discriminate based on pollen spectra, plant macrofossils from packrat middens enabled reliable identification of modern biomes from arid and semiarid regions (provided a weighting factor was included for trees and shrubs). Pollen data together with plant macrofossils are frequently used in 'biomization' (Jolly et al., 1998; Tarasov et al., 1998; Elenga et al., 2000) where it has also been argued (Janská et al., 2017) that direct comparisons between such data-models require uniformity in global paleodata. The utility of macrofossils as direct indicators of both paleotemperatures and vegetation types has been questioned in certain fossil floras due to the preponderance of traits such as toothed leaves in wet-soil environments that affect the outcome of leaf physiognomically based temperature estimates (Kowalski and Dilcher, 2003). Further, while pollen and macrofossil records are useful for landscape-scale reconstructions around a specific site, by themselves they can be less well suited to reconstructing spatial patterns of different vegetation types across broader areas (Huntley and Allen, 2003; Janská et al., 2017).

Fossil charcoal is included here as an element within the macrofossil spectrum both in macro- and micro-form. Due to its origin, charcoal is intimately associated with fire and therefore typically applied as an indicator of fire frequency and intensity (Hopkins et al., 1993; Valencia et al., 2018). Microscopic charcoal was used successfully to reconstruct fire history through an analysis of lake sediments in Japan (Inoue et al., 2001) and showed good indicator value when combined with pollen and phytolith data in a study of wet–dry paleosequences in the St Louis estuary in Minnesota (Nurse et al., 2017). As with other fossil elements, plant species identification and vegetation type based on fossil charcoal tend to be calibrated against woody material in extant floras. Charcoal fragments collected from soil under tropical rainforest in North Queensland, Australia, were matched against wood samples of extant *Eucalyptus* species from the region in a study that revealed strong indications that pyrophytic *Eucalyptus* woodlands occupied previously large areas of all the extant humid rainforest massifs between approximately 27,000 BP and 3500 BP (Hopkins et al., 1993, 1996). Depending on the level of abundance and structure, charcoal may contaminate other fossil elements thus reducing its potential indicator value as well as that of other associated fossil elements (Bonnefille et al., 1995).

6.2.7. Leaf margins

In modern ecology leaf margins tend to be relegated as a subsidiary trait to more readily analysable leaf functional attributes. In paleoecology however, leaf margins take on a very different level of significance where they are generally classified either as entire or non-entire, the latter being further defined as 'toothed'. Whether a margin is toothed or not depends on the diagnostic criteria. Gentry (1969) for example, considered a non-entire leaf to be one with "readily discernible" margin serrations, although 'discernibility" can be problematic (Greenwood, 1992). Altogether nine classes of teeth (including one lobed with teeth) were described by Wolfe (1993) who noted that, among other functional traits, teeth function as hydraulic pumps throughout the lamina. Trends in the adaptation of leaves to cooler climates are well established in literature as a function of mean annual temperature (MAT) where cooler conditions support leaves with larger, more numerous teeth, and tend to be more highly dissected (Bailey and Sinnott, 1916; Boeger et al., 2004; Royer et al., 2005; Hinojosa et al., 2010; Peppe et al., 2011), (SI Fig. 2). Studies by Royer et al. (2005) indicate that many physiognomic variables correlate significantly with MAT suggesting a coordinated, convergent evolutionary response of fewer teeth, smaller tooth area, and lower degree of blade dissection in warmer environments. In addition, tooth area correlates negatively with leaf mass per area and positively with nitrogen content. As well as temperature, there is evidence to support the adaptive significance of teeth to leaf thickness and deciduousness, thus providing a functional link to thin leaves and the deciduous habit (Royer, 2012; Royer et al., 2012). Overall, functional attributes of leaf teeth are well documented. Toothed species for example, correlate significantly with traits associated with the 'fast-return' end of the leaf economics spectrum (LES), including leaf nitrogen, low leaf mass-per-area, deciduousness and ring porous wood (Royer, 2012; Royer et al., 2012). The possibility that leaf teeth might have a role in increasing transpiration (Bailey and Sinnott, 1916; Wolfe, 1993), is also supported through an observation in leaf water management by Feild et al. (2005) who showed that hydathodes in leaf teeth prevent flooding of intercellular airspaces via guttation of a basal angiosperm *Chloranthus japonicus* (see also Wolfe, 1993). Subsequently, Royer and Wilf (2006) also confirmed that rates of photosynthesis and transpiration in teeth of woody dicotyledonous species in a North American deciduous forest were higher in plants native to a colder climate, and based on these functional criteria (gas exchange and photosynthesis), argued a case for their inclusion in methods of assessing paleotemperatures.

Because the physiognomy of herbaceous angiosperms is considered to be less sensitive to climate, leaf margin analyses tend to be calibrated more with woody dicots (Bailey and Sinnott, 1916; Peppe et al., 2011). Although there is a lack of consensus in how data should be analysed, several methods are well documented, one of these being the Climate–Leaf Analysis Multivariate Program CLAMP (Wolfe, 1993; Kovach and Spicer, 1995; Yang et al., 2011) that has been applied widely in paleoclimatic reconstruction (Gregory-Wodzicki, 2000; Spicer et al., 2003; Uhl et al., 2007; Tomsich et al., 2010). The Leaf Margin Analysis tool of Greenwood (1992) includes multiple traits including life form, and multivariate data analysis to derive a "foliar physiognomic signature" to better elucidate data otherwise confounded by taphonomic constraints. Digital leaf physiognomy (DLP) on the other hand, uses multiple variables to reconstruct climate (Royer et al., 2005; Peppe et al., 2011), while species range maps of native North American dicot trees and leaf margin types were used by Adams et al. (2008) to derive synthetic local flora. Additionally, Corney et al. (2012) describe a novel Leaf Measurement Algorithm to automate the marginal tooth analysis of leaves found in digital images.

The application of leaf margin analysis in paleoclimate and vegetation reconstructions is not without its critics. The assumption of convergence required for precise, quantitative temperature estimates using present-day leaf traits for example, is not supported by empirical evidence, resulting in very limited confidence in previously published, numerical paleotemperature estimates (Little et al., 2010). Furthermore, in certain residual fossil environments, due to taphonomic biases and few species numbers, estimates of leaf margin type can be highly variable thus affecting the accuracy of paleotemperature interpretations based on leaf margin alone (Greenwood, 1992). Evidence for the combined influence of MAT and multiple traits such as leaf thickness and leaf habit suggest that leaf margin type is controlled independently by these traits indicating that paleoclimate and vegetation reconstruction estimates may be flawed if these factors are not taken into account. Local conditions may also have a significant influence on the outcome of leaf physiognomically based temperature estimates where, for example, floras of predominantly wet-soil environments show a greater than expected proportion of toothed leaves (Kowalski and Dilcher, 2003). The use of extant floras in hindcasting paleotemperature (and associated vegetation type) is also further confounded by differing paleofloristic histories and phylogenetic disparities between regions (Hinojosa et al., 2010; Jacques et al., 2011; Peppe et al., 2011; Kunzmann et al. this volume).

6.2.8. Leaf size (area)

Leaf size (here considered as one-sided area of the lamina) has received much attention in the paleo literature as a potentially useful indicator of paleotemperatures and to some degree paleovegetation reconstruction. The functional relationships of leaf size with the physical environment are nonetheless subject to some debate. Leaf size may vary directly with mean annual temperature (MAT) (Wright et al., 2007; Gallagher et al., 2011; Moles et al., 2014) or (more generally) with available moisture expressed as precipitation (mean annual rainfall) (Givnish, 1984; Keshet et al., 1990; Wolfe, 1993; Wilf et al., 1998; Jacobs, 1999; Malhado et al., 2009; Royer, 2012). Larger leaves will be warmer than smaller leaves because of their thicker boundary layer, but for this reason are more vulnerable to night time chilling as they impede convective exchange with the surrounding air (Lusk et al., 2018). Convective relationships defined by leaf size and indumentum largely determine the manner in which a leaf responds to or can acclimate to environmental change. Because higher leaf temperatures increase transpiration more dramatically than photosynthesis, large leaf construction becomes prohibitively expensive in dry environments. Furthermore, as small leaves tend to have a higher density of major veins, they should be less vulnerable to hydraulic disruption such as embolisms and thus tolerate drought better than most large leaves (Scoffoni et al., 2011; Royer, 2012). Developments in scaling relationships in leaf venation and climate allow estimation of intact leaf size from fragments and this can arguably lead to improved hindcasting of past climate and biodiversity from fossil remains (Sack et al., 2012). More generally, size-dependent scaling of leaf support investments depends on plant life form and climate (Niinemets et al., 2007).

Through modeling the balance of leaf energy inputs and outputs, Wright et al. (2017) showed that daytime and night-time leaf-to-air temperature differences are key to interpreting geographic gradients in leaf size (see also Roth-Nebelsick and Konrad, this volume, Section 4.3). This finding helps to explain the predominance of large-leaved species in hot, humid, sunny environments where small-leaved species typify hot, arid, sunny conditions while also occurring in high latitudes and elevations. Depending on how leaf size is characterized, leaf size traits may carry different degrees of functional information. For example, broad laminas help confer competitive exclusion while morphologically large leaves can, through dissection, be functionally small. In addition, although leaf size scales positively with plant size, many of the largest-leaved species are of medium height with basally supported leaves (Hodgson et al., 2017). Leaf size can change markedly depending on local vegetation dynamics. For example, leaf size in treefall gaps and secondary successions in many tropical and temperate forest mosaics is typically much larger than in more established vegetation stages.

Compared to oldgrowth forest and adjoining savannas for example, large leaves in rapidly changing successional sequences are typically shorter-lived with high carbon acquisition rates (Gillison, 2013; Lusk and Laughlin, 2017). In such gradients, leaf area-based photosynthetic traits are known to be associated with tree height and the degree of leaf drought stress, even in diverse tropical rain forest trees (Kenzo et al., 2015). Within tropical forests in general, leaf size typically decreases towards the canopy and in seasonal forests tends to be accompanied by an increase in deciduous species and compound leaves (Popma et al., 1988; Gillison, 2013). Within the 'normal' spectrum of leaf size–-temperature relationships, there are notable divergences where, for instance, large thin leaves avoid excessive solar irradiance by adjusting inclination of the lamina. This is evident in the occurrence of large pendulous leaves in semi-arid to arid environments (Curtis et al., 2012) and in moist tropical forests with short-lived, 'high acquisition' leaves in secondary successions (Gillison, 2013). Conversely, large pendulous leaves in high latitudes may be seeking rather than avoiding irradiance (Wolfe, 1993), and thus both phenomena have implications for paleoclimate inferences. Functional trade-offs in the leaf size–inclination relationship are becoming increasingly well documented where inclination as an offset to irradiance can be shown to be more important to plant maintenance than, for example, acquiring leaf nitrogen (Posada et al., 2009) or maximising carbon gain (Myneni et al., 1986; Falster and Westoby, 2003; Wang et al., 2007).

Both MAT and frost-free period were found by Lusk et al. (2018) to be good predictors of evergreen angiosperm leaf size in forest assemblages, but no climate variable predicted deciduous leaf size. Although winter deciduousness makes large leaves possible in strongly seasonal climates, large-leaved evergreens are largely confined to frost-free climates for reasons outlined above. According to Lusk et al. (2018), evergreen leaf size data can therefore be used to enhance vegetation models, and to infer paleotemperatures from fossil leaf assemblages. However, atmospheric influences such as elevated CO_2 on leaf size can also cause an increase or decrease or remain unchanged in woody C_3 species thus creating difficulties for a correction factor in estimates of paleoclimate (Gregory, 1996). Variation in tropospheric ozone concentrations can also influence leaf area within populations of the same species and the degree to which the plant succeeds in acclimating to ambient oxidative pressure, especially where ozone can alter the competition among genotypes and favour the more resistant (Bussotti, 2008). Depending on the species, increase in total leaf area per plant may vary with certain life forms. In Brazilian savannas for example, forest trees accumulate leaf area more rapidly than savanna trees, thereby accelerating the transition to forest (Hoffmann et al., 2012). Taphonomic influences in paleoclimates may render habitat definition and species assemblages problematic where forest floor leaf litter is markedly local in origin and is taxonomically biased towards leaves from canopy trees and where litter has smaller leaves than expected from the canopy, using either specimen- or taxon-based observations (Greenwood, 1992).

While climate is a proximal driver of leaf size, nutrient availability also has a major influence on leaf size and many associated traits. In general, leaf size decreases with decreasing nutrient availability, especially phosphorus and nitrogen and with increasing dryness. Such leaves are typically evergreen, sclerophyllous with low carbon assimilation rates at the low end of the leaf economic spectrum and are relatively long-lived. Small leaved plants tend to dominate in very low nutrient environments such as savannas (Beard, 1953; Beadle, 1967; Gillison, 1983; Tomlinson et al., 2013) or Mediterranean vegetation types such as Fynbos (Cowling and Campbell, 1980) and Brazilian Campos Rupestres with all such vegetation types attracting the term 'peinobiome' (Mucina, 2018a). Similarities can be drawn here in certain moist or semi-aquatic substrates such as acidic peat moorlands (Kamiyama et al., 2014). In this discussion, other related influences of substrate such as salinity (Eallonardo et al., 2012), leaf and stem succulence are excluded due to their general absence in the fossil record as paleoreconstruction indicators. Considered overall, there are many obstacles in using leaf area to infer paleoclimate where even if a fossil flora is 100 percent validly determined, inferences of paleoclimate remain problematic (Wolfe, 1993). When combined with other functional traits as indicated in a modal PFT syndrome (see Section 8. and Gillison, this volume), leaf size can become a significant indicator of local species pools. For paleovegetation reconstruction this would require specific fossil evidence of co-occurring functional traits that would allow the construction of a PFT syndrome.

6.2.9. Herbivory

The long-term response of plants and insect herbivores can be interpreted by analyzing insect herbivore damage on well-preserved fossil angiosperm fossil leaves (Currano et al., 2016; also Kunzmann et al., this volume, Section 3.6). The system of foliar insect damage typology (Labandeira et al., 2007) depends largely on fossil examples because there is no similarly detailed classification in the standard ecological and entomological literature (Adams et al., 2011) (although see Lowman, 1984). Diversity in leaf damage by insects has been shown to vary directly with changes in temperature to the extent that anomalous changes in such a pattern can be used to infer past ecosystem

disruptions (Wilf and Labandeira, 1999; Wilf, 2008; Adams et al., 2011). Previous studies (Wilf et al., 2005; Smith, 2008; Currano et al., 2010; Adams et al., 2011) showed that shifts in damage type diversity on fossil leaves during the latest Cretaceous and early Palaeogene were positively correlated with paleotemperature proxies. Not surprisingly perhaps, overall insect herbivory, plant richness, and herbivorous insect diversity are widely considered to be greatest in the tropics, implying broad correlations between temperature and plant diversity, insect diversity, herbivory, or all three (Janzen, 1970; Connell, 1971; Stork, 1987; Coley and Barone, 1996; Labandeira and Currano, 2013; Currano et al., 2016). While the assumption of direct scaling of folivory with temperature underpins many studies of insect damage in paleovegetation (Wilf and Labandeira, 1999; Labandeira et al., 2002; Wilf et al., 2001; Wilf, 2008) this assumption is not supported in extant vegetation where detailed analyses of insect herbivory along global and continental latitudinal gradients reveal either an inverse relationship between insect folivory and temperature (Adams and Zhang, 2009; Moles et al., 2011) or else no evidence at all for change (Andrew and Hughes, 2005).

It is argued (Björkman et al., 2011) that higher predator pressure in warmer climates may partly explain the observed inverse patterning of folivory and latitudinal temperature. It is also likely that cascades of functional traits affecting folivory–climate relationships, include highly complex plant–herbivore defence interactions where plants continue to evolve strategies to balance gains in carbon assimilation against costs in the establishment and maintenance of chemical and biophysical defence mechanisms and where diversity in such strategies tends to vary directly with temperature (*cf*. Moles et al., 2011). Variation in leaf size is thus associated with major changes in within-leaf support investments and in large modifications in integrated leaf chemical and structural characteristics. Such size-dependent variations have a significant effect on general leaf structure *versus* function scaling relationships and demonstrate important life-form effects on and climatic differentiation in foliage support costs (Niinemets et al., 2007). For these reasons, and in the absence of other co-occurring fossil evidence of confirmatory functional traits, herbivory has limited application as an indicator of vegetation response to paleoclimate. Apart from paleoclimate, models simulating likely influences on vegetation performance under future climate change rarely include factors such as reduction of leaf mass through folivory. Yet, as suggested by Wolf et al. (2008), herbivory may cause alterations in vegetation structure that can change predictions of future forest composition.

7. Plant functional indicators of vegetation response to present and future climates –A question of scale

The value of plant functional indicators of vegetation response to climate is necessarily purpose- and scale-dependent. While climate alone is the principal driver of vegetation dynamics globally, at progressively finer geospatial scale, the ultimate composition and structure of species and functional types is subject to increasingly complex cascades of energy (light), nutrient and moisture availability on varying substrates. These in turn are influenced by human intervention and naturally occurring biophysical phenomena. In assessing plant functional indicators of climate change therefore, the primary question is – which climate and non-climate related variables can be linked to a specific purpose and scale? In vegetation science 'scaling' can refer to the dependent variation of an organism's form or function in which the most commonly used scaling equation is the power function, as well as the use of empirical models of trait-based, response–effect interactions that can be scaled up or down, for example, across biome, landscape and forest canopy, to leaves and their components. The well-known leaf economic spectrum (LES) (Wright et al., 2004) describes scaling functions for leaf functional traits that relate to global primary productivity and nutrient cycling. Similar scaling analogues have been proposed for wood (Chave et al., 2009) and leaf venation (Blonder et al., 2011). While these strategies reveal scaling trends along global environmental gradients, all are concerned primarily with bivariate rather than multivariate relationships and as such run the risk of oversimplifying and thus masking significant plant–environment interaction at a variety of environmental scales (Gillison, 2013).

Inferences about species distributions based on single-trait spectra can be misleading when environmental gradients sort species by filtering multiple independent traits simultaneously (Jager et al., 2015). When matched against mean annual temperature at global scale, specific leaf area (SLA) (the reciprocal of leaf mass per unit area or LMA) shows a characteristic linear response (Wright et al., 2004) indicating 'slow' to 'fast' resource acquisition strategies in plant function. At increasingly finer scale however, SLA response can be mediated by a range of other functional traits to the extent that the SLA value becomes either less meaningful or else a misleading indicator of community or ecosystem response to environment (Foster and Brooks, 2005; Golodets et al., 2009; Chaturvedi et al., 2011; Gillison, 2016; Polley and Wilsey, 2018). Many plant species that share similar SLA values (in parentheses below) can differ markedly with respect to life form or PFT, for example, the evergreen tree *Nothofagus betuloides* ($59.7\,cm^2\,g^{-1}$), the deciduous grass *Hierochloe alpina* ($58.8\,cm^2\,g^{-1}$) and an evergreen shrub (chamaephyte) *Vaccinium vitis-idaea* ($56.1\,cm^2\,g^{-1}$) or species with completely different metabolic pathways such as the CAM hemicryptophytic succulent *Sedum acre* ($50.0\,cm^2\,g^{-1}$) and the C_3 tree *Pistacia lentiscus* ($49.4\,cm^2\,g^{-1}$) (A.N. Gillison unpublished and other sources). For these reasons alone, SLA, LMA and related LDMC (leaf dry matter content) require careful consideration when used as isolated traits in models that aim to predict vegetation composition under climate change. Instead it would seem more logical to select alternative sets of traits and PFTs that, *in toto* discriminate more meaningfully between plant functional groups and do so on a whole-plant basis (Section 9). Varying suites of traits have been suggested for scaling up from organ to ecosystem such as the 'functional markers' of Garnier et al. (2004) using three leaf traits, SLA [$m^2\,kg^{-1}$], LDMC [$mg\,g^{-1}$] and N concentration [$mg\,g^{-1}$]. Adequate field-testing of these and other scaling-up approaches at global scale (Körner, 1994; Hodgson et al., 1999; Niinemets et al., 2007) is still a subject for debate where, at reduced scales, local edaphic influences and land use history can override the influence of climate especially where N or P are limiting (Sala et al., 2000; cf. Reich and Oleyksn, 2004).

8. Trait selection for forecasting vegetation composition under climate change

The selection of plant functional traits and types for the purpose of analyzing and subsequently forecasting the composition and performance of vegetation assemblages is inevitably influenced by an understanding of trait contribution to fitness under well defined habitats. Overall fitness is achieved through adaptive strategies that ensure a net benefit between increased gains in carbon assimilation and the costs of resource acquisition. Theories underlying strategies in resource acquisition and expenditure are well described for example, in the LHS and LES strategies already noted in the foregoing (Westoby, 1998; Wright et al., 2004; Díaz et al., 2016). In this context mention should be made of the CSR (Competitors–Stress–Ruderal) strategy as it applies to biomes (Grime, 1977; Pierce et al., 2017). The Leaf–Life form–Root (LLR) strategy described by Gillison (2013) complements the CSR, LHS and LES systems that otherwise exclude significant photosynthetic traits such as leaf inclination (Falster and Westoby, 2003; Posada et al., 2009), leaf phyllotaxis or insertion pattern such as rosettes (Withrow, 1932; Lavorel et al., 1998, 1999; Diaz et al., 2007; Bernhardt-Römermann et al., 2011) and green-stem photosynthesis (Gibson, 1996; Gregory, 1996; Pfanz, 1999; Lüttge, 2008), all of which constitute important plant adaptations to irradiance, nutrition and water availability and are thus relevant to any discussion on vegetation response to climate change.

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For the purposes of this paper it is necessary to provide some explanation of the background and theory underpinning the use of PFTs. Under the LLR, plant functional traits such as leaf size class assume additional functional significance when combined with leaf-inclination and other morphological (e.g. leaf stomatal distribution) and temporal (leaf longevity) descriptors of photosynthetic tissue. In this paper, photosynthetic attributes describe a 'functional leaf' as any part of the vegetative plant (including the primary stem cortex but excluding fruit and below-ground roots) capable of carbon assimilation. Unlike most other systems that infer global trends in plant functional performance, LLR also includes succulent vegetation that involves significant elements of world flora mainly in arid environmental extremes (*ca*. 10,000 species; Oldfield, 1997). In the LLR system specific trait syndromes or PFTs are termed plant functional *modi* (Gillison, 1981) representing whole-plant functional modality (*cf*. Violle et al., 2007). Functional *modi* described hereafter as 'modal PFTs', are constructed using an assembly-rule set and syntactical grammar based on 36 generic plant functional elements (PFEs) (Gillison and Carpenter, 1997; Gillison, 2002) (SI Fig. 3, Table 2). The system comprises a many-to-many mapping whereby more than one modal PFT can be represented within a species and vice versa. A typical modal PFT for an individual of *Acer palmatum* for example, might be a mesophyll (*me*) leaf size class with pendulous (*pe*) inclination, dorsiventral (*do*) (hypostomatous), deciduous (*de*) leaves with green-stem (cortex) (*ct*) photosynthesis supported by a phanerophyte (*ph*), the resulting modal PFT combination being coded as *me-pe-do-de-ct-ph*. Change in any one element of the modal construct for the same species, such as an increase in leaf size (e.g. mesophyll to notophyll) along a moisture gradient, results in a new modus (*no-pe-do-de-ct-ph*). Thus the method is sensitive to intraspecific variation under environmental change and thereby well suited to detecting and potentially forecasting vegetation response to climate change. The methodology is described in detail elsewhere (Gillison, 2002, 2013) and can be readily applied in practice using the VegClass software package (Gillison, 2002). A numerical functional 'distance' matrix between modal PFTs can be generated in VegClass and used directly in comparing and analysing plant assemblages at multiple scales (Fig. 1, Table 2). A global data set compiled using a standard recording proforma covering all major latitudes and climates that support plant growth (Gillison, 2018) indicates that a realistic approximation of unique modal PFTs is ≈3500 or about one percent of the world's approximately 350,000 vascular plant species.

Unlike many methods that employ so-called 'hard' functional traits (i.e. those requiring detailed instrumental and time-consuming laboratory techniques) the traits used in the present system are readily observable in field in addition to being science-based (Gillison, 2002). The methodology has been applied successfully in identifying indicators of biodiversity and vegetation types and their environmental determinants within and between continents and across different latitudes (Gillison, 2012, 2013, 2016, 2018). The purpose of this and other methods described below, is to assemble and analyse data acquired at plot level and aggregated at global scale to identify plant functional traits and types as potentially useful predictors of vegetation composition under present and future climate change. Both the methodology and analytical outcomes at global and regional scale are described in Part II (Gillison, this volume).

9. Discussion

For past vegetation, a review of literature undertaken for the purpose of this study, has shown that the complexities involved in the assessment of paleovegetation and habitat, often with very limited data, create a significant challenge for retrodictive vegetation modeling. This is particularly evident when hindcasting vegetation reconstruction is necessarily matched against what may be unproven functional performance of extant taxa and habitats. Paleovegetation studies at biome scale and their methods of construction utilize many PFTs defined in part by climate terminology that lack a useful measure of functional significance, in addition to being open to circular reasoning. As such they are unlikely to have any relevance at local community or ecosystem scale. Yet it is at the community level where the processes involved in the interaction and integration of functional attributes determine the ultimate structure and composition of plant assemblages – processes that, in turn, are influenced directly or indirectly by extrinsic environmental factors such as climate. To understand how vegetation responds to climate change therefore is to understand the processes involved at community scale including interaction with the biophysical habitat. It is for this reason that modal PFTs as used in this and the following paper (Part II, Gillison, this volume) while of potential application at biome scale (cf. Bigelow et al., 2003; Royer, 2012; Binney et al., 2017), are likely to be of much lesser value in hindcasting paleovegetation reconstruction at finer scales given the uncertainties in habitat delineation outlined above.

A review of methods likely to show promise in the use of plant functional characteristics entailed an examination of case studies in which PFTs had been used in paleovegetation reconstruction. Almost all case studies reviewed, involving hindcasting vegetation reconstruction, mainly in Holocene environments, focus on biome rather than local community scale. The reasons for this become obvious when many taphonomic constraints are combined with other related problems in determining the origins and timing of the stratographic sequencing of fossil sites. This, in turn, raises questions about the validity and accuracy in defining paleo plant habitat. Increasing numbers of plant ecological studies focus on intraspecific phenotypic plasticity in which the functional morphology of a species phenotype can change significantly along a biophysical gradient and as a function of neighbouring species composition (Abakumova et al., 2016). To detect such variation on a paleo scale with fossil plant material does indeed present a challenge. Yet such phenomena are critical elements in the construction and maintenance of vegetation types. The indeterminate nature of much fossilized plant and animal residue, especially in multiple strata of complex origins, can place severe limits on the accuracy and validity of hindcasts of vegetation reconstruction based on functional traits. Constraints in PFT definition can become problematic therefore, when using extant taxa especially where intraspecific variation can be shown to vary with habitat. Such variation is likely to be significant with respect to determining the indicator value of a species or PFT for vegetation reconstruction purposes. Compared with characterizations of present day terrestrial habitats, defining paleohabitat especially at local scale, thus presents its own unique challenges where the validity of estimates of the ecological relationship between habitat and plant community is not without question.

The largely uncritical and pervasive use of biomization procedures remains a challenge in achieving consistency in describing and classifying vegetation response to changing environments across multiple scales. As shown in the foregoing, prevailing inconsistencies in PFT classification and circular reasoning arise from the use of PFT descriptors that combine extrinsic abiotic habitat descriptors with functional traits that are often vague or broad-ranging (grass, tree, shrub etc.). Given these limitations it is perhaps unsurprising that, as described by Elenga et al. (2000), there is as yet no general consensus in the acceptance of a unique and global biomization scheme. At a more specific functional level, the widespread acceptance of individual functional traits in ecological studies described in the foregoing, relies on largely untested assumptions that certain traits operate independently of others within and between individual plants. This paper has reviewed several studies which demonstrate that one of the most widely used 'orthogonal' traits such as SLA is indeed open to mediation by other traits or at least shows functional inconsistencies across differing life forms. Apart from manipulative experiments in mainly cropping systems, there is a general lack of experimental data in natural vegetation that describe and quantify trait interaction at whole-plant level. This highlights a fundamental need to determine what rules

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should apply to constructing a specific trait assemblage for a whole-plant syndrome or functional modus that, for practical purposes, allows an expression of trait coordination and potential interaction and avoids undue reliance on individual traits. The LLR strategy describes one such possibility that aims to couple science with practice through the construction of a parsimonious set of generic elements of resource acquisition and conservation that apply globally. Clearly this kind of approach will require further testing and modification as more data come to hand with advances in ecophysiology coupled with field tests at multiple environmental scales. The underlying ecological principles embodied in an approach of this kind are nonetheless relevant to modeling vegetation response to changing climates as well as other largely uncontrolled factors such as species acclimation, invasive and pathogenic organisms, land use change and human population pressure.

10. Conclusions

The use of plant functional types and traits in paleovegetation reconstruction may be applicable at biome scale but is unlikely to be of value at finer geospatial and temporal scales due in part to uncertainties in paleohabitat definition, fossil dispersal and the difficulty of matching extant PFTs and related taxa as proxies for paleoenvironmental modeling. Predictive models that rely on biomization of limited sets of inadequately defined PFTs are likely to generate misleading outcomes at biome scale while ignoring finer scale yet critical detail at individual plant or ecosystem level. Compelling empirical evidence of trait interaction and coordination at whole-plant level points to a strong case for the use of modal PFTs rather than an over-simplistic reliance on isolated individual functional traits whose values are often expressed only as questionable community means. For models that aim to predict vegetation response to climate change, these trends suggest that in the selection of model parameters, the devil will lie in the functional detail. As Part I of a two-part presentation (Gillison, this volume), this overview has addressed several important trends in the way plant functional types and traits are being applied as indicators of vegetation response to climates across temporal scales. While the trends identified are presented as a template for further research, they point to a number of key questions that may be expressed as emerging hypotheses:

1) A whole-plant system of modal plant functional types (PFTs) based on a core set of functional strategies of resource acquisition and conservation, can provide an improved alternative to PFTs and traits used so far in models of vegetation response to climate change;
2) Modal PFTs are more efficient indicators of vegetation response to climate change than individual traits;
3) Improved plant functional selection criteria can lead to improved parameters in Earth System and Dynamic Global Vegetation Models.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.flora.2019.03.013.

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